THE ICHTHYOSAURIAN TAIL: SHARKS DO NOT PROVIDE AN APPROPRIATE ANALOGUE

by C. McGOWAN

ABSTRACT. The lunate caudal fin, characteristic of post-Triassic ichthyosaurs, is often interpreted as functioning as a reversed shark's tail, generating vertical as well as horizontal components. The functional morphology of the shark's tail is discussed, and considered far from well understood. Although the ichthyosaurian tail is superficially similar to a reversed heterocercal tail, the two structures are not strictly analogous and there are functional grounds why the ichthyosaurian tail should not generate vertical forces. The selachian tail is therefore unsatisfactory, and alternate models are sought among cetaceans and scombroid fishes.

Bone density in ichthyosaurs appears low, as in cetaceans, suggesting they were positively buoyant, at least while close to the surface. Diving may have been initiated by a downward flexing of the body, as Taylor (1987) suggested, and the increasing hydrostatic pressure, by reducing lung volume, would probably soon have eliminated positive buoyancy. The pectoral fins were probably used as inclined planes, adjusting swimming levels. The pelvic fins may have functioned as stabilizers, though their effects may have been marginal because of their small size. That ichthyosaurs evolved a downturned rather than an upturned tail may have been entirely fortuitous.

A CHARACTERISTIC feature of post-Triassic ichthyosaurs is the possession of a tailbend, a downward flexion of the vertebral column in the posterior caudal region. Examination of the remarkably well preserved 'skin' specimens, where the body outline is preserved as a carbonaceous film, shows that this downturned segment supported the ventral lobe of a lunate caudal fin. The body shape is thunniform, like that of dolphins and scombroid fishes, and there seems little doubt that these ichthyosaurs were similarly adapted for fast cruising (Webb 1988; Massare 1988). Most of these skin specimens are from the Lower Jurassic (Upper Liassic) of the Holzmaden area of southern Germany, and belong to several species of the genus *Stenopterygius* (Text-fig. 1). Other genera, including *Ichthyosaurus* from the English Lower Liassic, have similar skeletal anatomies, indicating that they too had thunniform bodies, and this appears to have been typical of Jurassic and Cretaceous ichthyosaurs. Triassic ichthyosaurs, in contrast, were predominantly long-bodied, and were not adapted for fast cruising (Massare and Callaway 1990). The present account, based solely on material from the Lower Jurassic, is only concerned with thunniform ichthyosaurs.

Although essentially symmetrical externally, the ichthyosaurian tail is markedly asymmetrical internally because the dorsal lobe is without any skeletal support. Such a condition is the exact reverse of the heterocercal tail, and the ichthyosaurian tail has accordingly been interpreted as functioning like an inverted shark's tail (Grove and Newell 1936; McGowan 1973, 1983; Taylor 1987). Before examining the propriety of such treatments, it is necessary to understand how the tail functions in sharks.

According to standard textbook accounts of sharks (e.g. Young 1962), the forward propulsive thrust of the tail is accompanied by a vertical upthrust. The resulting upthrust tends to pitch the head downwards, but this negative pitch is counterbalanced by the upthrust generated in front of the centre of mass by the pectoral fins, functioning as inclined planes (Grove and Newell 1936; Harris 1936; Alexander 1965, 1968). This swimming mechanism is intuitively satisfactory because it accounts for how negative buoyancy, once thought to be characteristic of sharks, is overcome, thereby enabling them to regulate their position in the water. However, Thomson (1976) pointed out that many sharks are neutrally buoyant, and he questioned the assumption that the heterocercal
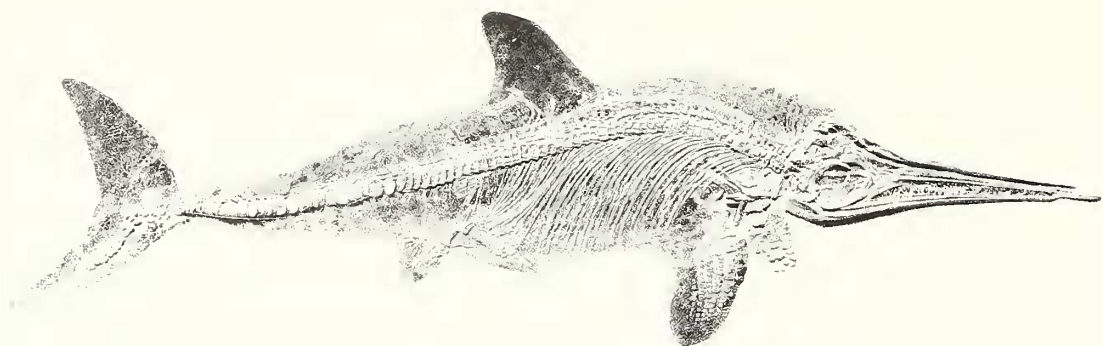
TEXT-FIG. 1. *Stenopterygius quadriscissus*; BMNH R4086; an ichthyosaur skeleton from the Lower Jurassic (Upper Liassic) of Holzmaden, southern Germany.

tail always generates an upthrust. By reviewing the results of other investigators, and by making some of his own observations on living sharks, Thomson concluded that the heterocercal tail did not generate a lift force that caused a negative pitching of the head. Instead, the tail produced a forward thrust that was inclined downward through, or close to, the centre of mass (Thomson 1976; Thomson and Simanek 1977). This was said to cause an overall sinking effect which would be counterbalanced by the lift generated by the pectoral fins.

Thomson's work on sharks was a major influence on Taylor's (1987) reassessment of the swimming mechanism of ichthyosaurs. Since Taylor's study is the most recent, and, I believe, the most satisfactory account of ichthyosaurian locomotion, it is necessary to examine its underlying premises. The first objective of the present paper is therefore to assess the functional morphology of the heterocercal tail of sharks, with particular reference to Thomson's work, to see whether it is appropriate to treat the ichthyosaurian tail as a reversed shark's tail. Other models for the ichthyosaurian tail will then be examined, namely cetaceans and scombroid fishes. After considering the question of buoyancy, an attempt will be made to assess the function of the tail and to see how ichthyosaurs may have swum.

MATERIALS AND METHODS

Several preserved sharks were examined, all in the Department of Ichthyology and Herpetology, Royal Ontario Museum, abbreviated ROM, together with some fresh sharks caught on a Department of Fisheries and Oceans cruise. Some of the ichthyosaurs studied were also in the collection of the ROM, but references are also made to specimens in other collections. Abbreviations used are: BMNH, The National History Museum, London, formerly called the British Museum (Natural History); BSPM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; FSF, Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt; GPIT, Geologisch-Paläontologisches Institut Tübingen, Germany; MHH, Museum Hauff, Holzmaden, Germany; OUM, Geological Collections, University Museum, Oxford; PMUU, Paleontologiska Institutionen, Uppsala Universitet, Sweden; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YPM, Peabody Museum of Natural History, Yale University. Some of the specimens cited were without catalogue numbers and are referred to by manuscript numbers, given in quotation marks.

Values for the angle of the tailbend for different ichthyosaur species were taken from McGowan (1979). The angle of the tailbend is the acute angle measured between a horizontal line drawn through the atlas vertebra and the apex of the tailbend, and a line drawn from the apex of the tailbend to the tip of the tail (McGowan 1972). The assumption was made that the specimens from which the tailbend data were derived had authentic tailbends that had not been altered during

preparation. Previous investigations have shown that this is not always a safe assumption (McGowan 1989, 1990a). However, since verification requires dismantling each specimen, which is usually not possible, there is no alternative but to accept the tailbend data at face value, noting that there could be some inaccuracies.

Aspect ratios were calculated from photographs of the tails of skin specimens using the relationship: aspect ratio = span²/area. Span was measured to the nearest 0·01 cm using dial callipers. Area was deduced (cm²) by weighing graph paper cut-outs of the tail outlines and comparing these with cut-outs of known area (Fierstine and Walters 1968). The accuracy of the method was tested by measuring the area of a tail cut-out, obtained by counting squares, and comparing this with the estimate obtained by weighing. The error was found to be 1·5 per cent. As with the tailbend data, the assumption was made that the carbonaceous outlines of the tails were authentic. However, it is recognised that this is not necessarily so, and that some tails may have been embellished during preparation (Martill 1987). Some of the individual aspect ratios reported here may therefore be inaccurate.

Bone density in ichthyosaurs was assessed by examining three specimens in which the internal structure of the bone was visible. All three were collected from the Lower Liassic (Hettangian and Sinemurian) of Lyme Regis, Dorset: YPM 3145, an isolated forefin of *Ichthyosaurus communis* which has a natural transverse fracture through the shaft of the humerus; ROM 12814, a partial skeleton of *Ichthyosaurus communis* which had previously been serially sectioned; and ROM 328, a vertebral centrum of *Temnodontosaurus* which has a natural transverse fracture. For comparison, transverse sections were cut through the humeri of the following Recent aquatic mammals that are known to have dense bone: *Hippopotamus amphibius* (ROM R1171); *Trichechus manatus*, manatee (ROM R439); and *Phoca hispida*, ringed seal (ROM R1881); together with *Delphinapterus leucas*, beluga or white whale (ROM 19974) which, like other cetaceans, lacks dense bone.

TAIL MORPHOLOGY AND FUNCTION IN SHARKS

There is much variation in the shape of the tail among shark species. Large and active pelagic forms, like the porbeagle, *Lamna nasus*, and the white shark, *Carcharodon carcharias*, have tails with a high aspect ratio (the span of the tail divided by its average width) and a steeply upturned vertebral column. Smaller, less active species, like the smooth dogfish, *Mustelus canis*, and the spiny dogfish, *Squalus acanthias*, have low aspect ratio tails in which the vertebral column is more gently angled (Text-fig. 2). These variants, however, all conform to the same general pattern (Text-fig. 3), the
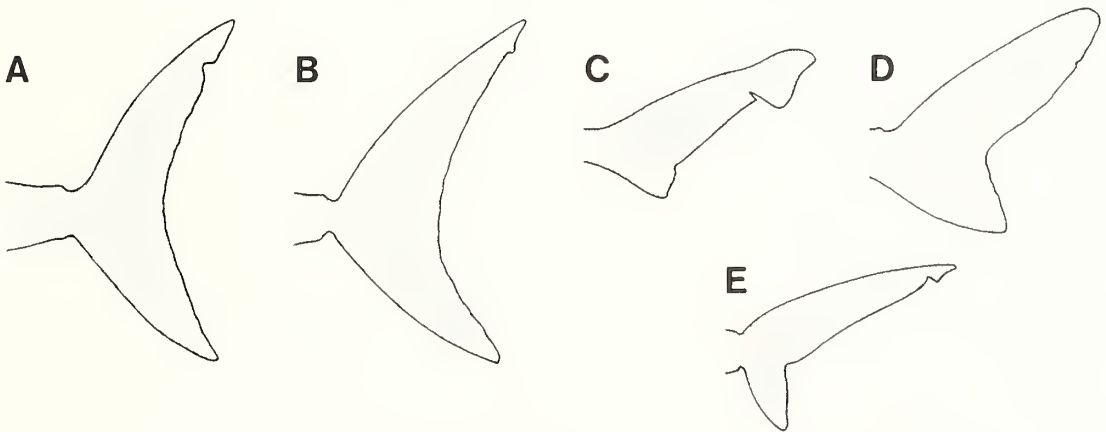
TEXT-FIG. 2. Tails of various sharks showing differences in aspect ratio and in the angle at which the vertebral column is upturned. A, the porbeagle, *Lamna nasus*. B, the white shark, *Carcharodon carcharias*. C, the smooth dogfish, *Mustelus canis*. D, the spiny dogfish, *Squalus acanthias*. E, the hammerhead shark, *Sphyrna lewini*.
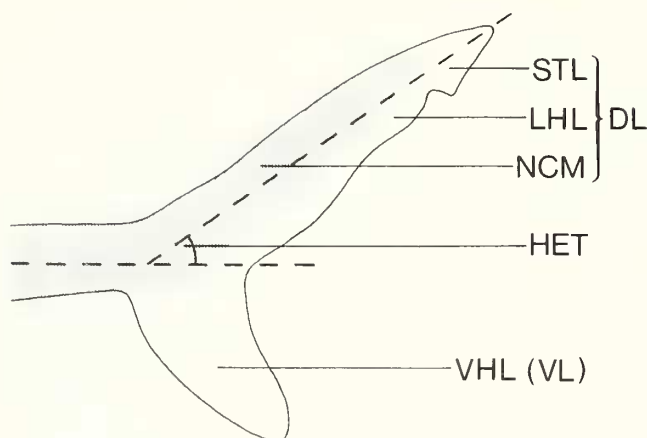
TEXT-FIG. 3. A generalized shark's tail showing the major anatomical features. The longitudinal hypochordal lobe (LHL), notochordal mass (NCM), and subterminal lobe (STL) together form the dorsal lobe (DL). The ventral hypochordal lobe (VHL) may be referred to simply as the ventral lobe (VL). The heterocercal angle (HET) is the angle that the notochordal mass subtends to the horizontal.

description of which follows the terminology used by Thomson (1976) and Thomson and Simanek (1977). The upturned vertebral column, with its associated musculature, comprises the *notochordal mass*, and the angle that this subtends to the horizontal is referred to as the *heterocercal angle*. Immediately beneath the notochordal mass lies an elongate fin lobe, the *longitudinal hypochordal lobe*. In many species this lobe is separated by a notch from a small distal entity called the *subterminal lobe*. Ventrally and proximally is the *ventral hypochordal lobe*. For convenience the notochordal mass, with its attached longitudinal hypochordal and subterminal lobes, may be referred to as the dorsal lobe; the ventral hypochordal lobe as the ventral lobe.

The conventional model

The conventional understanding of tail function in sharks attributes the generation of upthrust to the fact that the ventral lobe is not as stiff as the dorsal lobe. Consequently, as the tail is moved from side to side, the more pliant ventral lobe is deflected, becoming an inclined plane that generates lift (Text-fig. 4). Alexander (1965) demonstrated this using a simple apparatus in which an amputated tail could be rotated in the horizontal plane. He used the tails of two small and readily available species: the dogfish, *Scyliorhinus caniculus*, and the tope, *Galeorhinus galeus*. In both species the ventral lobe is more pliant than the dorsal lobe. Consequently, when the tail is rotated, the ventral lobe is deflected by the resistance of the water and functions as an inclined plane to generate a continuous upthrust. Although this experiment was conducted on only two species (with similarly shaped tails) there has been a tendency to interpret the results as being typical of *all* sharks. There
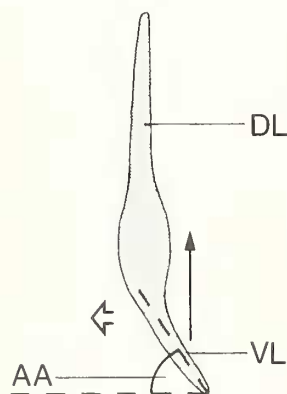
TEXT-FIG. 4. Diagrammatic posterior view of a shark's tail, as it is being moved towards the left (direction of the open arrow) with respect to the animal. According to conventional wisdom the ventral lobe (VL), being more compliant than the dorsal lobe (DL), is deflected by the water. It therefore becomes an inclined plane moving at an acute angle of attack (AA), and thus generates an upthrust (solid arrow).

is also the problem that amputated tails may not function in the same way as living ones. The radial muscles in the hypochordal region, for instance, probably modify the action of the tail during swimming (Alexander 1965; Simons 1970), and this could have profound effects on the forces generated. The generalization that the ventral lobes of the heterocercal tail is more pliant than the dorsal lobe and consequently provides a device for generating lift is clearly not founded upon a wide range of species, and exceptions might therefore be expected.

Departures from the conventional model

Simons (1970) showed that the ventral lobe generates a downthrust in both the Port Jackson shark, *Heterodontus portusjacksoni*, and the piked dogfish, *Squalus megalops*. This was demonstrated using a modification of the apparatus used by Alexander (1965). Simons found that the removal of the ventral lobe *increased* the epibatic (lifting) effect of the tail, contrary to expectations of the conventional model. The explanation offered for this unexpected result is that when the tail is moved laterally the ventral edge of the ventral lobe leads rather than trails (Text-fig. 5). As a consequence,

TEXT-FIG. 5. Diagrammatic representation of the caudal fin of the Port Jackson shark (*Heterodontus portusjacksoni*) as it is being moved towards the left (with respect to the animal). A, lateral view of tail, moving towards the observer – the lines b–b and c–c indicate planes of section cut through the tail for the next two illustrations. B, posterior view of section cut through plane b–b as the tail moves towards the left (direction of the open arrow); notice that the extensive ventral lobe (VL) moves such that its ventral edge leads and therefore functions as an inclined plane moving at an obtuse angle of attack (AA). c, posterior view of section cut through plane c–c as the tail moves towards the left (direction of the open arrow); notice that the dorsal lobe (DL) moves such that the ventral edge trails and therefore functions as an inclined plane moving at an acute angle of attack (AA). D, dorsal view of the tail as it moves towards the animal's left (direction of the open arrow); the ventral edge of the ventral lobe (VL) and the dorsal edge of the dorsal lobe (DL) lead.
Modified from Simons 1970.
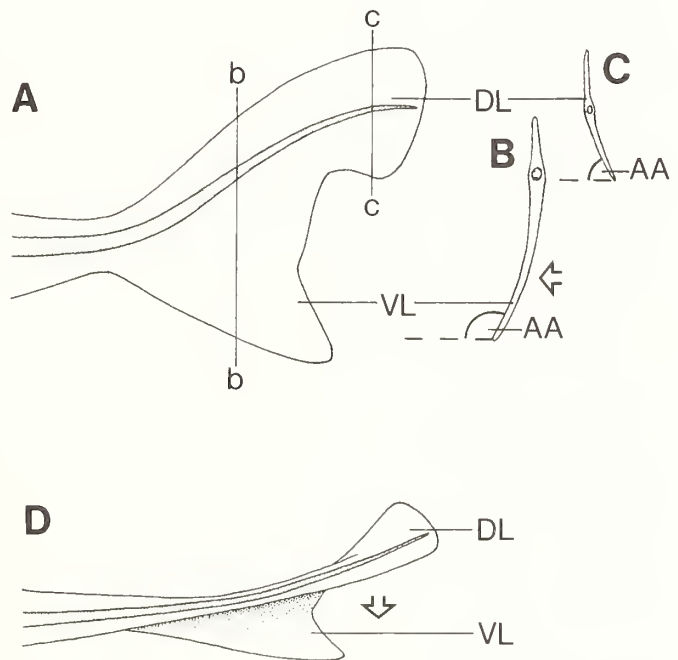
the ventral lobe acts as an inclined plane moving at an obtuse angle of attack, and therefore generates a downthrust. The dorsal lobe, in contrast, moves such that its ventral edge trails the dorsal edge. The dorsal lobe therefore acts as an inclined plane moving at an acute angle of attack, and therefore generates an upthrust. Removal of the ventral lobe, by removing the obtuse-angled plane, reduces the magnitude of the downthrust, thus increasing the epibatic effect of the tail. The reason why the tail of the Port Jackson shark assumes this shape when moved from side to side in the water is not apparent from an inspection of preserved material. Several specimens were examined (ROM 38675), but in each the ventral lobe appears as thin and flexible as the dorsal lobe.

Simon's experimental design showed that the forward thrust generated by the tail was directed obliquely upwards from the horizontal. The angle of elevation of this force 12° for

H. portusjacksoni and 26° for *S. megalops* – was dependent upon the relative sizes of the dorsal and ventral lobes, and upon the positions of their leading and trailing edges. Simons correlated these morphological differences with swimming performance. The Port Jackson shark is a slow-moving animal that feeds on molluscs and echinoderms, habitually swimming horizontally. Although capable of ascending, it can only do so at shallow angles, and this appears to be laborious. The faster-swimming piked dogfish, with its more steeply angled line of thrust, is capable of making steep climbs and dives.

Thomson's model

Thomson (1976) and Thomson and Simanek (1977) hypothesized that the thrust from the tail of sharks was not directed obliquely upwards, as Simon had described, but rather forwards and slightly downwards, to pass through, or close to, the centre of mass. This so called 'balanced thrust' was the resultant of two opposing caudal components: a downthrust generated by the dorsal lobe, and an upthrust. The upthrust was not attributed to the deflection of the ventral lobe – the conventional interpretation – but to the twisting of the entire tail about its longitudinal axis. It is now necessary to see how these two forces were considered to be generated.

Thrust generated by dorsal lobe. To visualize how the dorsal lobe generates a downthrust it is necessary to ignore the ventral lobe. Thomson (1976) suggests we begin by imagining that the vertebral column is not upturned but is, instead, perfectly straight (Text-fig. 6A). When the tail moves from side to side the dorsal lobe is deflected, forming an inclined plane that generates a forward horizontal thrust directed towards the head (Text-fig. 6B). Suppose the vertebral column is now tilted upwards, at the heterocercal angle. The dorsal lobe of the tail still gives a thrust towards the head, but, because this segment is now tilted at an angle to the horizontal, its thrust is directed downward (Text-fig. 6C).
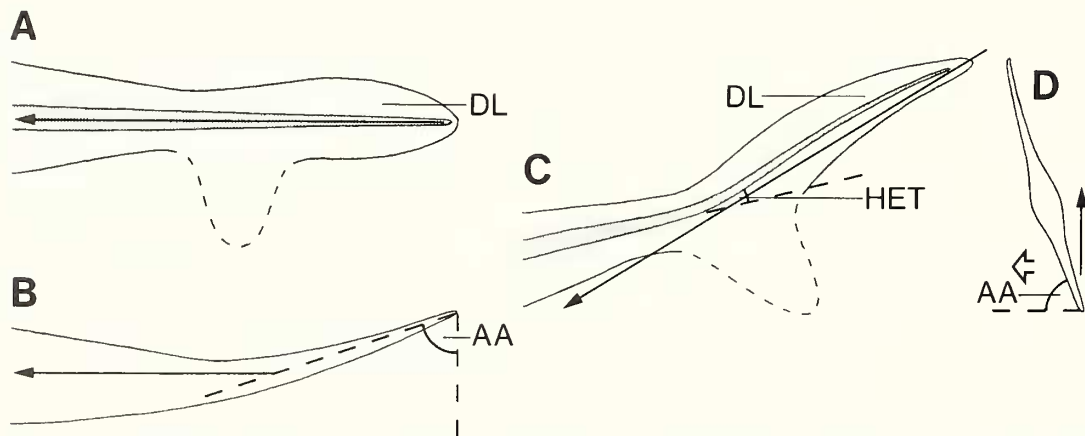
TEXT-FIG. 6. Visualizing the forces generated by the shark's tail according to Thomson's model. A, left lateral view and B, dorsal view, of a hypothetical shark's tail in which the vertebral column is not upturned. (For the sake of the argument the ventral lobe, shown by the broken line, is ignored.) When the tail moves towards the shark's left, the dorsal lobe is deflected by the water, forming a plane that is inclined at an acute angle of attack (AA). The thrust of this inclined plane is directed horizontally, towards the head (solid arrow), and has no vertical component. C, left lateral view of a shark's tail in which the vertebral column is upturned, at the heterocercal angle (HET). When the tail moves towards the shark's left the dorsal lobe (DL) still generates a thrust towards the head. However, since the dorsal lobe is angled from the horizontal, this thrust is directed downward (solid arrow). D, diagrammatic posterior view of a shark's tail, as it is being moved towards the left (direction of the open arrow). Rotation of the entire tail causes it to function as an inclined plane. As the angle of attack (AA) is acute, the tail generates an upthrust (solid arrow).

Thrust generated by the twisting of the whole tail. According to Thomson and Simanek (1977, Fig. 4B), the entire tail becomes twisted about the longitudinal axis when it moves laterally, such that the ventral edge of the ventral lobe trails behind the dorsal edge of the dorsal lobe (Text-fig. 6D). As a result the whole tail functions as an inclined plane moving at an acute angle of attack, and therefore generates an upthrust.

Heterocercal angles and the maintenance of a balanced thrust. The heterocercal angle is fixed for a given shark (though some adjustment is possible in the pitch of the whole tail through the caudal peduncle) and the steeper this angle, the greater is the downthrust generated by the dorsal lobe, up to some maximum. The compensatory upthrust generated by the twisting of the tail therefore has to increase with increasing heterocercal angle, in order to maintain a balanced thrust. Thomson (1976) deduced that a balanced thrust could only be maintained in sharks where the heterocercal angle did not exceed 33°. Sharks with more steeply upturned tails therefore required an additional epibatic effect. This was provided by the ventral lobe, which functioned as a trimming device. Its action was said to be similar to that of the dorsal lobe, but in the opposite direction, producing a forward thrust that was inclined upward rather than downward. This trimming action appeared to be confirmed by the positive correlation found between the areas of the ventral lobe and the heterocercal angle (Thomson 1976). However, as Webb (pers. comm.) has pointed out, a positive correlation between ventral lobe area and heterocercal angle is only to be expected on geometrical grounds. This is because the area available beneath the vertebral column increases with increasing angle, up to some maximum value, after which it decreases. Thomson (1976) obtained heterocercal angles and ventral lobe areas from the literature, and of the fifty-nine species assessed, most had angles of about 20° or less. Only five species had angles that exceeded 30°, the highest values being for the pelagic sharks: *Cetorhinus* (40°), *Carcharodon* (41°), *Lamna* (45°) and *Rhincodon* (52°). The area of the ventral lobe, which rarely exceeded 30 per cent of the total caudal fin areas, reached a maximum value of 45 per cent, in *Rhincodon*.

Thomson's (1976) epibatic role for the ventral lobe is consistent with the conventional model, but it should be remembered that the latter was based upon only a few species. Furthermore, both are at variance with the hypobatic (negative lift) function ascribed to the ventral lobe by Simons (1970). Thomson briefly discussed the discrepancy between his results and those of Simons, attributing this to the way in which the amputated tail was moved during Simons's experiment, but the explanation was not altogether satisfactory. Some doubt therefore exists regarding the functional role of the ventral lobe.

Relative stiffness of dorsal and ventral lobes

One feature not discussed by Thomson (1976), or by Thomson and Simanek (1977), is the variation in the relative stiffness of the dorsal and ventral lobes. My limited survey of preserved material at the ROM, and of fresh material, reveals much variation in this feature. For example, the spiny dogfish, *Squalus acanthias* (ROM 23930), has a low aspect ratio tail with a large and flexible dorsal lobe and a flexible but much smaller ventral lobe (Text-fig. 2D). The hammerhead shark, *Sphyrna lewini* (ROM 23319), has a high aspect ratio tail in which the dorsal lobe is compliant whereas the ventral lobe, which is about one third as large as the dorsal lobe, is rigid (Text-fig. 2E). A tail structure similar to *Sphyrna* was also seen in preserved material belonging to three species of the genus *Carcharhinus*: the silvertip shark, *C. albimarginatus* (ROM 43956); the oceanic whitetip shark, *C. longimanus* (ROM 28204); and the silky shark, *C. falciformis* (ROM 28205). Fresh material of the shortfin mako, *Isurus oxyrinchus*, and of the blue shark, *Prionace glauca*, showed a similar condition and a survey of other taxa would probably reveal additional examples.

The relative stiffness of the dorsal and ventral lobes would appear to be the major factor determining whether the horizontal swimming thrust is accompanied by an epibatic or a hypobatic component. However, Thomson (1976) concluded that the ventral lobe has the same function in all sharks, and that it always acts as a trimming device to reduce the hypobatic effect of the dorsal lobe. This conclusion was based on his observations of the swimming movements of three species: the

leopard shark, *Triakis semifasciata*; the sand tiger shark, *Eugomphodus taurus* (formerly *Odontaspis taurus*); and the brown shark, *Carcharhinus milberti*; and from his analysis of films of other (unspecified) species. The propriety of generalizing on the role of the ventral lobe on such a limited sampling is questionable, and exceptions are provided by the Port Jackson shark and piked dogfish (Simons 1970). The role of the ventral lobe should be investigated further.

This brief survey shows that the heterocercal tail of the shark is considerably more complex than was formerly considered and that our knowledge of its function is far from complete. This should be borne in mind when attempting to understand the functional morphology of the tail of ichthyosaurs – a group of animals that became extinct over eighty million years ago.

ICHTHYOSAUR TAILS AND MODERN ANALOGUES

The ichthyosaurian tail differs from that of a reversed shark's tail in two important respects. First, the skeletally unsupported lobe – dorsal in ichthyosaurs but ventral in sharks – is relatively much larger in ichthyosaurs than in sharks, though the discrepancy is less marked in thunniform sharks like *Lamna* and *Carcharodon* (Text-fig. 2A–B). Indeed, the two lobes have essentially the same area in ichthyosaurs, whereas in sharks the ventral lobe, as noted, rarely exceeds 30 per cent of the total tail area (Thomson 1976).

Since the area of the unsupported lobe in sharks increases with increasing heterocercal angles (Thomson 1976), could the relatively larger unsupported lobe in ichthyosaurs merely be attributed to their having relatively steeper-angled tails? Preservational problems make it difficult to measure tailbend angles in ichthyosaurs accurately, but most of the best preserved Lower Jurassic specimens (from the Holzmaden area of southern Germany) have angles similar to those of sharks (McGowan 1979). These include *Stenopterygius quadriscissus*, the commonest species (23–39°, mean value 27°); *S. hauffianus* (18–27°); *S. megalorhinus* (20–27°); and *S. megacephalus* (21–35°). In some instances the tailbend approaches 40°, but such steep angles are uncommon. *Eurhinosaurus longirostris* probably had the most steeply down-turned tail, but the angle of the bend is probably about 40° (McGowan 1990b) rather than as high as 54° as formerly believed (McGowan 1979; Riess 1986). Ichthyosaurs, then, do not have more steeply-angled tails than sharks, so their relatively larger unsupported (dorsal) tail lobe is not attributable to differences in angulation.

The second difference between the tails of sharks and of ichthyosaurs is that the skeletal support is bony rather than cartilaginous. Since bone is considerably stiffer than cartilage, it is likely that the skeletally supported ventral lobe was stiffer in ichthyosaurs than the equivalent dorsal lobe is in sharks.

One of the implications of ichthyosaurs having stiff tails was that their aspect ratios were fairly high (Table 1; Text-fig. 7). The other implications of these differences will be discussed later.

So far, the only neontological model for the ichthyosaurian tail has been the heterocercal tail of sharks, but two other tail forms need consideration, namely those of cetaceans and of scombroid fishes.

Cetaceans

Whales and dolphins have lunate tails which are externally symmetrical and which have no internal skeleton. Regardless of the lack of bony support, the flukes (tail lobes) are both stiff and tough. It has been reported that entire carcasses can be suspended by cables passed through holes cut in the flukes and that freshly excised cubes of tissue can withstand repeated blows of a heavy mallet (Felts 1966). These physical properties are attributed to their composite structure. There is a central core of dense fibrous tissues, comprising horizontal, vertical and oblique collagen fibres interspersed with fat cells, and this is sandwiched between two ligamentous layers. The ligaments of these more superficial layers fan out over the two surfaces of the flukes like contour lines on a map. They serve to resist tensile forces generated by the pressure of the water during propulsive movements of the tail. The tail moves dorsoventrally rather than laterally as in fishes and ichthyosaurs, but otherwise functions as an inclined plane in the same way.

TABLE 1. Aspect ratios of selected ichthyosaurs.

Name	Specimen number	Aspect ratio	Text-fig.
Stenopterygius hauffianus	GPIT 1491/4	4·57	7A
Stenopterygius megacephalus	FSF 457	3·69	7B
Stenopterygius megacephalus	OUM JZ163	3·52	7C
Stenopterygius quadriscissus	BMNH R4086	3·25	7D
Stenopterygius macrophasma	SMNS 16811	3·73	7E
Immature individual*	PMUU R435	4·08	7F
Immature individual*	MHH 'Q21'	3·56	7G
Immature individual*	BSPM ASI 559	3·06	7H
Immature individual*	MHH 'Q23'	4·33	7I
Immature individual*	GPIT 'Q07'	4·15	7J

* For reasons discussed elsewhere (McGowan 1979), immature individuals cannot be identified with any certainty. Immature individuals are ordered according to increasing jaw length (from 200 mm–340 mm).
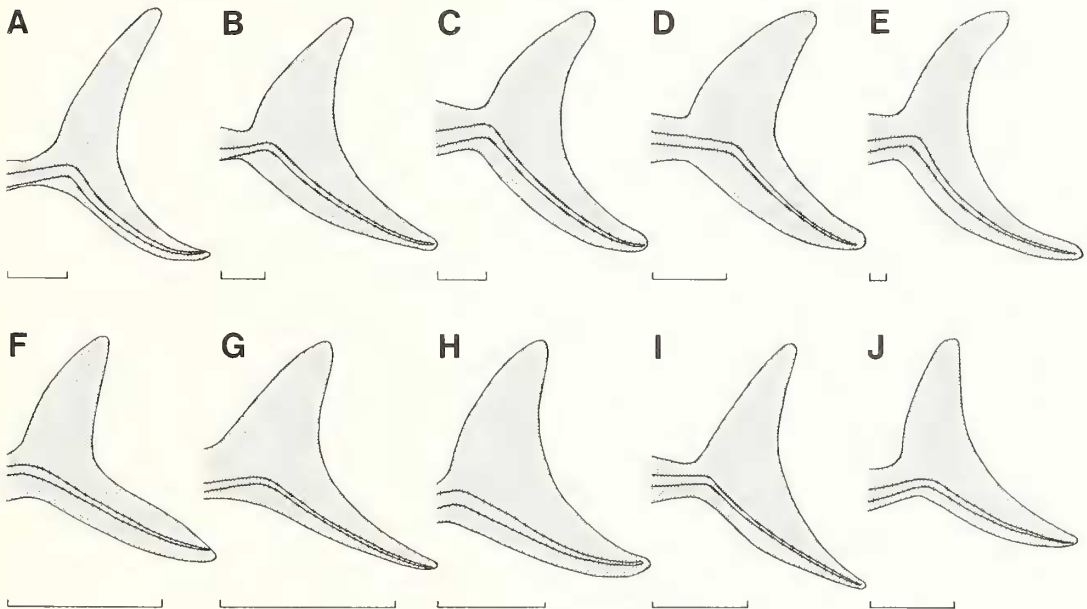
TEXT-FIG. 7. Tail shapes of selected ichthyosaurs, redrawn from photographs of their carbonaceous outlines. A, *Stenopterygius hauffianus*; GPIT 1491/4. B, *S. megacephalus*; FSF 457. C, *S. megacephalus*; OUM JZ163. D, *S. quadriscissus*; BMNH R4086. E, *S. macrophasma*; SMNS 16811. F–J, immature individuals: PMUU R435; MHH 'Q21'; BSPM ASI 559; MHH 'Q23'; GPIT 'Q07' respectively.

Observations of small cetaceans swimming in tanks show that the movement of the flukes are slightly out of phase with the vertical movements of the caudal region (Parry 1949b; Smith *et al.* 1976). The significance of this is that the flukes maintain an acute angle of attack throughout most of their up and down strokes, thus generating an almost continuous forward thrust. This movement requires a two-joint system, and the otherwise stiff cetacean body has two areas of flexibility (Text-fig. 8): one with a centre of rotation that is just posterior to the dorsal fin, and the other with a centre of rotation that is at the level of the anterior edge of the tail flukes (Parry 1949b). Parry (1949a) showed that the anatomical basis for these two centres of rotation lies in the
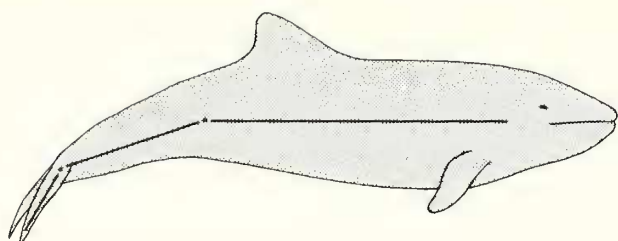
TEXT-FIG. 8. Diagrammatic representation of a cetacean to show that having a two-joint system permits the tail flukes to maintain an acute angle of attack relative to the water flow.

vertebral column. The lumbar region is stiff, and this is maintained by two ligaments, one dorsal the other ventral. The dorsal ligament attaches to the neural spines of the lumbar vertebrae, while the ventral ligament attaches to their centra. These two ligaments terminate just beyond the level of the dorsal fin, giving rise to the anterior zone of flexibility. The posterior zone of flexibility is contributed to by three factors: the vertebrae in this region have large intervertebral spaces relative to their diameters; the articular surfaces of adjacent centra are convexly rounded instead of being flat; and the body is extremely narrow at this point, facilitating dorso-ventral movements.

There has been some disagreement among specialists on the relative forces generated by the upstroke and the downstroke. According to Purves (1963, 1968) the upstroke is the power stroke, the downstroke merely being a passive recovery stroke. This conclusion was reached primarily on two lines of evidence: the flukes bend more during the downstroke than during the upstroke, and the epaxial muscle mass is approximately double that of the hypaxial muscles. Observations of swimming cetaceans led Smith *et al.* (1976) to a different conclusion. They found that forward thrust could be generated by the upstroke or the downstroke and that either stroke could exceed the force of the other, or the two forces could be equal. Similar conclusions were reached by Felts (1966).

Unequal forces between strokes would generate vertical forces due to the reaction of the water. For example, if the downthrust was more powerful than the upthrust during a particular cycle of the tail, there would be a net lift on the tail. It would seem from all this that cetacean tails, like those of sharks, are complex devices, probably capable of generating variable vertical forces, both epibatic and hypobatic.

Scombroid fishes

There are many parallels between the swimming mechanisms of cetaceans and of scombroid fishes. Both have thunniform bodies, which are characterized by their stiffness, streamlined shape, lunate tails and their narrow caudal peduncles. Scombroid fishes also have a two-joint tail mechanism. Both of the joints arise as bony modifications of the vertebral column, and are located fore and aft of the peduncle (Fierstine and Walters 1968). The peduncle, itself a modified section of the vertebral column, is frequently drawn out laterally into a pair of bony keels which contribute to the lateral stiffness of the peduncle.

The caudal fin has an extensive internal skeleton of bony rays, and these are bound together by connective tissue and fine muscle fibres. The structural integrity of the fin, coupled with the inherent stiffness of the bone from which it is constructed, yields a structure of sufficient rigidity to support a high aspect ratio. Fierstine and Walters (1968) gave aspect ratios that ranged from between 4·19 and 6·63 ($N = 2$) for the swordfish, *Xiphias gladius*, to a remarkable 10·26 for a Pacific sailfish, *Istiophorus greyi*. For comparison they gave values of 2·50 for a Bottlenose dolphin, *Tursiops truncatus*, and 4·85 for a Common dolphin, *Delphinus delphis*. The highest aspect ratio reported here for an ichthyosaur is 4·57 (Table 1).

Reif and Weishampel (1986) found a number of parallels between scombroid fishes and lamnid sharks. Thus, lamnid sharks have a caudal peduncle with lateral keels, and they identified a double joint system. They concluded from this that lamnid sharks have all the attributes for oscillatory propulsion, unlike other sharks where forward thrust is generated by undulation. However, as the tail is cartilaginous, it lacks the stiffness of the scombroid tail and has a correspondingly lower

aspect ratio. They gave values of 2·99 and 3·25 respectively for specimens of a porbeagle, *Lamna nasus*, and a shortfin mako, *Isurus oxyrinchus*.

Cetaceans and scombroid fishes both provide better analogues for ichthyosaurian locomotion than sharks, but neither one is a perfect match. Thus cetaceans are like ichthyosaurs in the possession of lungs, and both groups lack the extremely high aspect ratio tails achieved by scombroid fishes. However, in contrast to ichthyosaurs, the cetacean tail lacks an internal skeleton of bone and its movements are dorsoventral rather than lateral. In both of these regards scombroid fishes are similar to ichthyosaurs. Choosing between a cetacean and a scombroid model is therefore inappropriate, and both models should be considered when discussing the swimming performance of these unique extinct reptiles.

BUOYANCY, TAIL FUNCTION, AND SWIMMING IN ICHTHYOSAURS

The belief that the ichthyosaurian tail generated a downthrust had much to do with the question of body density. Like Grove and Newell (1936), I assumed that ichthyosaurs, being air-breathers, were buoyant in water, and interpreted the tail as a device for generating a compensatory downthrust during submergence (McGowan 1973, 1983). While many air-breathers, ourselves included, do have densities that are less than that of water, it is not universally true. Many aquatic animals, including sirenians, most seals, the hippopotamus and the otter, have densities that are similar to, or slightly greater than, that of water. Their high densities are primarily due to their very dense bones, and this has been shown by cutting sections through their limb bones (Wall 1983). The functional significance of this is that these animals attain neutral or even negative buoyancy, in spite of any residual air in their lungs, and therefore do not have to expend energy to remain submerged. Cetaceans, surprisingly, do not have dense bones, and when they are swimming at the surface their density is less than that of the water (Wall 1983). However, prior to diving, they lose their positive buoyancy by expelling most of the air from their lungs. Because they tend to dive deeply their lungs collapse under the mounting water pressure, so their density soon exceeds that of water.

Examination of the bone histology of Lower Jurassic ichthyosaurs reveals that the bone is very porous, like that of cetaceans, in marked contrast to the high density bones of the other Recent vertebrates that were examined (Text-fig. 9). This suggests that ichthyosaurian bone probably had a low density and that their bodies may have been positively buoyant, at least while they were close to the surface. However, on diving it seems likely that this positive buoyancy would have been lost, as suggested by Taylor (1987), especially if they dived deeply.

Whether the horizontal propulsive thrust of the ichthyosaurian tail was accompanied by vertical components depends upon how the dorsal and ventral lobes behaved in water. If the skeletally unsupported dorsal lobe was compliant, it would probably have been deflected by the resistance of the water and acted as an inclined plane moving at an obtuse angle of attack, generating a downthrust. Similarly, if the ventral lobe was compliant, it would have been deflected by the water and acted as an inclined plane moving at an acute angle of attack, generating an upthrust. If the dorsal lobe was more compliant than the ventral lobe – which seems reasonable since the latter had a bony supporting skeleton – the tail would have generated a net downthrust (Text-fig. 10A). Conversely, if the ventral lobe was more compliant, which seems unlikely in view of its bony skeleton, the tail would have generated a net upthrust (Text-fig. 10B). A third alternative is that the unsupported lobe was inflexible, like that of a hammerhead shark, and that the two lobes were equally stiff, as in scombroid fishes and cetaceans. Such a rigid tail would have generated no vertical forces (Text-fig. 10c). Note that none of these scenarios takes into account any changes in the shape of the tail that may have been caused by contraction of the caudal muscles. Nor do they consider the possibility that the whole tail may have been twisted during swimming, as described for sharks by Thomson (1976) and by Thomson and Simanek (1977). Notwithstanding these uncertainties it seems that the most likely of the three alternatives is that ichthyosaurs had uniformly stiff tails, like those of cetaceans and scombroid fishes. This is inferred from three lines of functional evidence. First, on the evidence of the skin specimens, the ichthyosaurian tail had a moderately high aspect
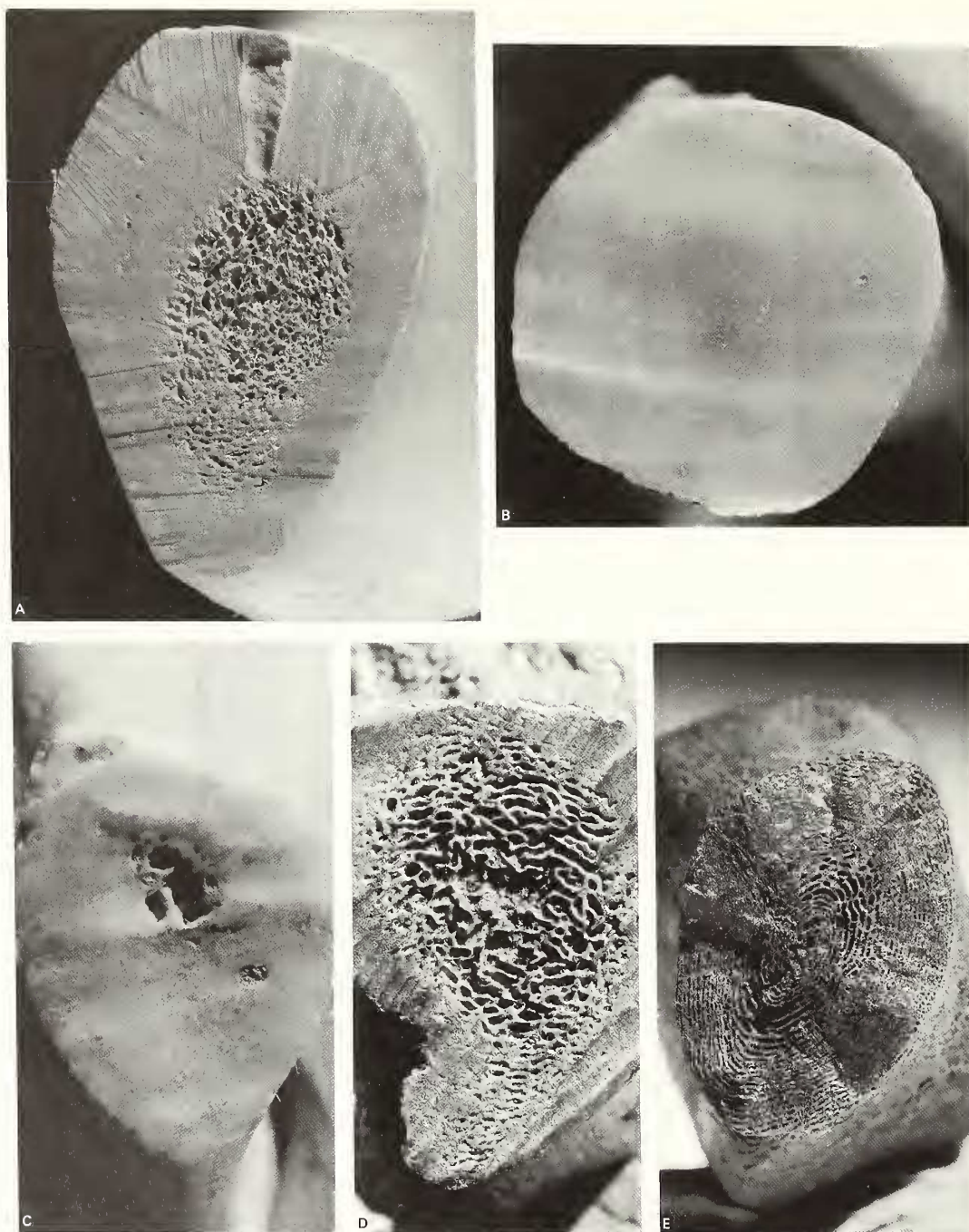
TEXT-FIG. 9. Transverse sections through the humeri of Recent aquatic mammals (A–D) and through a Lower Jurassic ichthyosaur (E). A, *Hippopotamus amphibius*; ROM R1171. B, *Trichechus manatus*, manatee; ROM R439. C, *Phoca hispida*, ringed seal; ROM R1881. D, *Delphinapterus leucas*, beluga or white whale; ROM 19974. E, *Ichthyosaurus communis*; YPM 3145.

TEXT-FIG. 10. Hypothetical alternatives for the behaviour of the dorsal and ventral lobes of the ichthyosaurian tail. In each case the tail is depicted as moving towards the left (open arrow), and is viewed from behind. A, if the dorsal lobe were more compliant than the ventral lobe its deflection would have been the larger, and the downthrust would have been greater than the upthrust of the ventral lobe (solid arrows). B, if the ventral lobe were more compliant than the dorsal lobe, its deflection would have been the larger, and its upthrust would have exceeded the downthrust of the dorsal lobe. C, if dorsal and ventral lobes were both stiff, no vertical forces would have been generated.
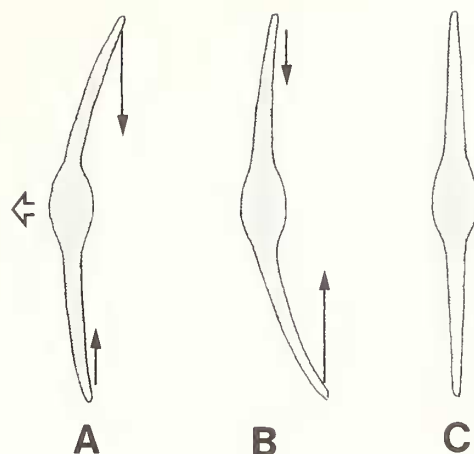
ratio – higher than reported values for sharks and sometimes comparable with values given for *Xiphias* (Table 1) – and this requires stiffness. Second, once an ichthyosaur had dived and presumably lost its positive buoyancy, a tail that generated no vertical components would appear to have been more advantageous than one that generated a downthrust (Text-fig. 11). Third, the cetacean and scombroid models are more in accord with the ichthyosaurian body, which, by virtue of its bony skeleton, is presumed to have been stiff.

Like scombroid fishes (Fierstine and Walters 1968), cetaceans (Parry 1949*b*), and lamnid sharks (Reif and Weishampel 1986), ichthyosaurs probably had a two-joint system in the axial skeleton to facilitate tail movements. There are no clearly demarcated skeletal features to indicate an anterior joint. However, the post-pelvic vertebrae have small neural spines, with even smaller chevrons, suggesting mobility throughout the caudal region, though movement was probably restricted to a prescribed centre of rotation by ligaments, as in cetaceans. A posterior joint may be represented by the marked change in diameters of the vertebral centra that occurs at the apex of the tailbend (McGowan 1974).

Taylor suggested that diving may have been initiated in a surface-swimming ichthyosaur by a downward flexure of the caudal region of the body. This would have raised the line of thrust of the tail above the centre of mass, producing a strong downward pitching of the head. Once an ichthyosaur was below the surface, changes in its horizontal swimming level were probably effected by using the pectoral fins as inclined planes (Text-fig. 11B–C). The pelvic fins may also have been used for the same purpose, though they may have functioned as stabilizers instead. Like the pectorals, the pelvic fins were probably inclined obliquely downwards from the horizontal, something like the flight feathers of a dart or arrow, and, like flight feathers, they were placed behind the centre of mass (Text-fig. 11D). They would therefore have functioned as inclined planes when the body deviated from a straight path, generating correcting forces that would tend to bring the body back onto a straight course. If their orientation was oblique they would have corrected for pitching (up-and-down) as well as for yawing (side-to-side) movements. The main role of the pelvic fins, then, may have been for stability rather than for changing swimming levels, though their relatively small size suggests that the role may have been of minor importance. Harris (1938), for example, found that the pelvic fins of the dogfish, which are about one-fifth the area of the pectorals, had a negligible effect on stability. This was partly because of their relatively small size, and also because of the interference of the flow over their surface caused by the downwash from the pectoral fins. A similar situation may well have pertained in ichthyosaurs. In *Stenopterygius*, for example, the forefin is usually at least twice as long as the hindfin (McGowan 1979), giving an areal difference of about four.
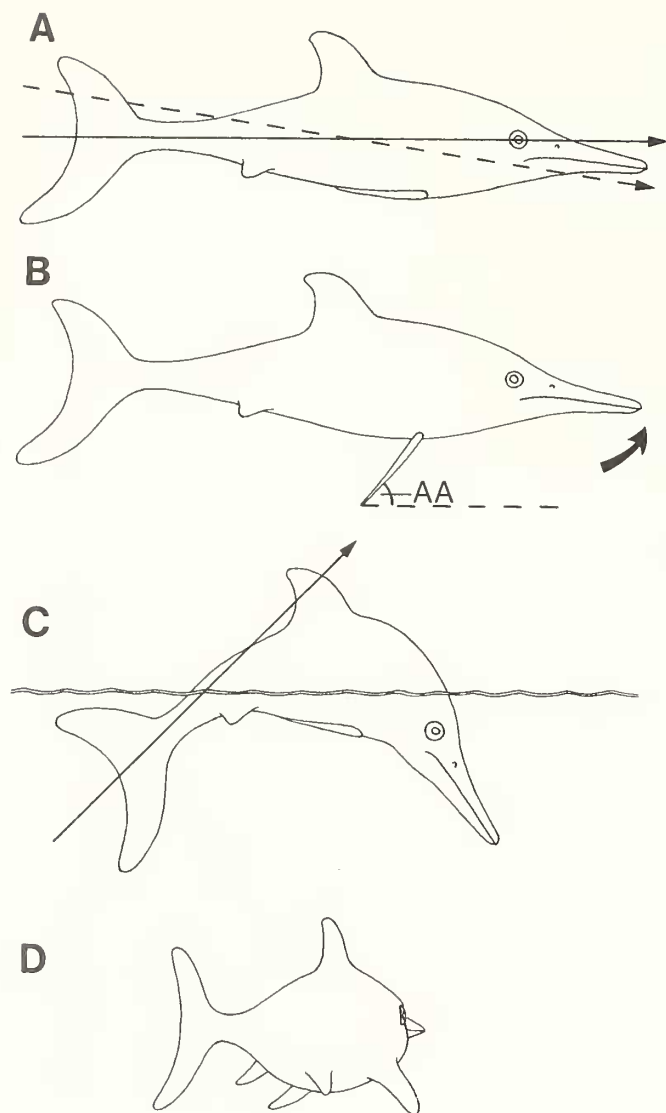
TEXT-FIG. 11. Swimming scenarios for thunniform ichthyosaurs. A, if the caudal fin had generated a net downward component, the forward thrust of swimming would have been inclined downwards (broken arrow), facilitating diving. If there had been no vertical components, which seems the most likely situation, the forward thrust would have been directed horizontally (solid arrow). B, changes in horizontal swimming level were probably effected using the pectoral fins as inclined planes. Upward pitch would have been achieved by setting the fins at an acute angle of attack (AA). C, diving in a surface-swimming ichthyosaur may have been initiated by flexing the body to produce a strong negative pitching movement of the head. D, the pelvic fins, like the pectorals, probably extended obliquely from the body, and their main role may have been for stability rather than for changing levels.

The proposal to replace the conventional selachian model of ichthyosaurian locomotion underscores the fact that ichthyosaurs, in contrast to sharks, had lungs and therefore had variable buoyancies because of changes in hydrostatic pressure. An animal whose buoyancy changed from positive to negative would seemingly derive less benefit from a tail that generated a unidirectional vertical component than one that generated only a horizontal component. If, then, the selection pressures for the evolution of tail asymmetry in ichthyosaurs had nothing to do with the generation of vertical forces, what other pressures may have been involved? Faced with similar problems among the bony fishes, Webb and Smith (1980) proposed that the essential feature in the evolution of caudal fin asymmetry during the early history of bony fishes was an increase in caudal fin depth. This would have resulted in increased fin area, hence improved fast-start performance. Similar pressures may have been operational during the early evolution of ichthyosaurs. Whether this was the case is unknowable, but if it were so it suggests that the evolution of a downturned vertebral

column may have been serendipitous and that an upturned tail may have been an equally likely evolutionary pathway for ichthyosaurs to have followed.

SUMMARY AND CONCLUSIONS

Given the uncertainty regarding tail function in living animals, the possibility of correctly interpreting ichthyosaurian tail function seems remote. Even if our interpretations were correct, we have no means of knowing it because our inferences cannot be tested. All we can do is to suggest possible functions for the tail, based upon living analogues. In previous studies, the reversed heterocercal tail of the shark has been regarded as the closest analogue for the ichthyosaurian tail. However, the resemblance between the two tail forms, namely the inflected vertebral column, is only superficial and closer inspection reveals important differences. More appropriate analogues for the ichthyosaurian tail are the stiff, high aspect-ratio tails of cetaceans and scombroid fishes. These models are more satisfactory than the selachian one because ichthyosaurs, in contrast to sharks, had lungs and therefore a variable buoyancy, and presumably had stiff bodies. The evolution of the ichthyosaurian tailbend may have had nothing to do with the generation of vertical forces, and an upturned vertebral segment may have been equally as likely as a downturned one.

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C. McGOWAN

Department of Vertebrate Palaeontology
Royal Ontario Museum, Toronto
Ontario, Canada, M5S 2C6
and
Department of Zoology
University of Toronto, Toronto,
Ontario, Canada M5S 1A1